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Seed development in the genus Peperomia*

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(WITH PLATES 3–6 AND A TEXT FIGURE)

The abnormal embryo sac is doubtless the most interesting feature of the development of the ovule and seed in the genus *Peperomia*. The first sixteen-nucleate embryo sac, found in Angiosperms, was that discovered by Campbell (6) in 1899, in *Peperomia pellucida*. Johnson (30), in 1900, first described the origin and development of the endosperm in *P. pellucida*. He showed that the mature embryo sac of this species contains one egg, one synergid, six nuclei which are cut off singly about the periphery of the sac and which finally degenerate, and eight nuclei which fuse to form the endosperm nucleus. Campbell (7), in 1901, confirmed the work of Johnson in all these features, except the number of synergids, which he thought might often be two. Schnegg (64), in 1902, reported a sixteen-nucleate embryo sac in *Gunnera*, a genus of the Haloragidaceae not at all closely related to *Peperomia* of the Piperaceae. Johnson (32), in 1902, showed that two species of the closely related genus *Piper* have typical eight-nucleate mature embryo sacs. In 1907, Johnson (34) described a new type of mature embryo sac in *Peperomia hispidula*, which likewise contained one egg and one synergid, but in which all the remaining fourteen nuclei fuse to form the endosperm nucleus. Ernst (21), in 1908, reported a sixteen-nucleate sac in *Gunnera macrophylla*. In 1908, Brown (4) reported, for three more

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species of *Peperomia*, embryo sacs essentially similar to that of *P. pellucida*, and also discovered evanescent walls following the first and second nuclear divisions in the sac. Miss Stephens (70), in 1909, described sixteen-nucleate embryo sacs for three different genera of the Penaeaceae, a family not closely related to the Piperaceae or the Haloragidaceae. Modilewski (50 and 52), in 1909 and 1911, found sixteen-nucleate sacs in two species of the Euphorbiaceae, which again are not closely related to any family in which this type of embryo sac had hitherto been found. Johnson (35), in 1910, reported a typical eight-nucleate sac in another species of *Piper*. Samuels (59), in 1912, extended the work of Schnegg and of Ernst on the genus *Gunnera*.

Since 1899, sixteen-nucleate embryo sacs, in which the arrangement of nuclei differs considerably in the different species, have therefore been found to occur in at least a half-dozen genera, distributed among four very distantly related families of Angiosperms.

In pursuit of additional evidence upon the significance of the abnormal embryo sac in the genus *Peperomia*, a study of the development of several species, not hitherto investigated, was undertaken. The species studied were: *P. reflexa* A. Dietr., *P. verticillata* A. Dietr., *P. scandens* Ruiz & Pav., *P. metallica* Lind. & Rod., *P. Fraseri*, var. *resediflora* C. DC., *P. blanda* HBK., *P. galioides* HBK., and *P. Langsdorffii* Miq. (?).

Piper tuberculatum Jacq., an arborescent species belonging to a very closely related genus, was also examined.

Most of the material used in this study was from Jamaican plants. It was in part collected from living plants in Jamaica,* and in part—the chief portion—from Jamaican plants growing in the greenhouse of The Johns Hopkins University at Homewood, which were brought back by The Johns Hopkins University Botanical Expedition of 1910.

The plants of *Peperomia scandens* and *Piper tuberculatum*, from which flower-spikes were collected, were directly determined by Dr. Casimir de Candolle from portions of the plants sent to him. The plants of *Peperomia reflexa*, *P. verticillata*, *P. metallica*, *P. blanda*, and *P. galioides* were carefully compared with herbarium specimens of these species, which had been determined by the same authority. The material of *P. Fraseri*, var. *resediflora* was obtained from a plant, labeled *P. resedaeflora*, in the greenhouse of the "Pflanzenphysiologisches Institut" in Munich.

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* The material was collected and fixed at Cinchona by Professor D. S. Johnson on visits made to Jamaica in 1903, 1906, and 1910. The expedition of 1903 was aided by a grant from the Botanical Society of America, that of 1906 from the Bache Fund, and that of 1910 from The Johns Hopkins University.

The material of the species which is here referred to as *Peperomia Langsdorffii* Miq. (?) was secured from a plant growing in the greenhouse of The Johns Hopkins University. This plant was obtained from the New York Botanical Garden, and their plant was secured from the "Königlichen Botanischen Garten," Dahlem, Germany, where it is known as *Peperomia humilis* (Vahl) A. Dietr., which is there considered to be equivalent to *Peperomia Langsdorffii* Miq. After an examination of a specimen of the Johns Hopkins plant and one of the New York plant, Dr. Casimir de Candolle thinks it can not be referred to *P. Langsdorffii* Miq., but that it is very probably a new species. However, in the absence of any other name, the plant will be referred to in this paper as *P. Langsdorffii* Miq. (?).

The material was killed and fixed in medium chromo-acetic, in acetic acid and absolute alcohol, or in Flemming's fluid. The first mentioned was generally the most satisfactory.

The stains used were Haidenhain's iron-alum haematoxylin, counterstained in Orange G; and Flemming's triple. The former combination was more satisfactory for the younger stages, while the latter was better for the later stages, in which the embryo and endosperm were formed.

For the sake of clearness, each species will be described separately, after which the general considerations will be taken up.

PEPEROMIA REFLEXA A. Dietr.

Peperomia reflexa A. Dietr., being typical of the series of Peperomias studied, will first be considered somewhat in detail. Part of the material of this species was collected on rocks at 5,000 feet elevation near Cinchona, where it grew on the dry south side of the Blue Mountains of Jamaica. Most of the material, however, was collected from two plants in the greenhouse of The Johns Hopkins University at Homewood. One of the greenhouse plants had been brought from Jamaica and the other had been collected by Professor C. J. Chamberlain in March, 1908, at Xalapa, Mexico.

The flower in this species consists of two stamens and a single carpel, which is sessile in the axil of a peltate bract (FIG. 4). These bracts, which are homologous with leaves, rather closely resemble in shape the peltate leaves of some other species of the genus (*e. g.* those of *P. arifolia*).

There is no evidence—not even rudiments—of calyx or corolla. The flowers are borne upon a terminal spike, which measures 15–25 mm. in length and 1.5–2.0 mm. in diameter. The flowers are arranged in such a close cylindrical spiral or helix that a cross-section of the spike frequently shows from five to seven flowers in almost the same plane. In the early stages the flowers are completely covered by the overlapping bracts, the upper edge of each bract being outside—a necessary result of the acropetal mode of development of flowers and bracts on the spike. In each carpel is borne a single, orthotropous ovule, with a single integument (FIG. 4). The sessile stigma, with its numerous finger-like papillae, is limited to the anterior or lower part of the carpel, the stylar canal opening just above the stigma.

The bracts and their axillary flowers have their origin in the periblem, and their development, so far as observed, very closely coincides with that described by Schmitz (63) for *P. urocarpa* Fisch. & Mey. (= *P. ionophylla* Griseb.).

The flowers are not only initiated in acropetal succession, but they reach maturity in the same order, there being a great deal of difference between those at the base and those at the apex of the spike, especially in the earlier stages of development. In this character the flowers of *Peperomia* are to be distinguished from those of the genus *Piper* in so far as the species examined in this study are concerned. In the latter the flowers originate acropetally on the spike, but they all reach maturity at practically the same time.

As is characteristic for all xerophytic species seen by the writer, each flower with its subtending bract is sunk in a depression in the inflorescence axis. The depth of the depression may practically equal, or even slightly exceed, the height of the ovule; and this relation obtains without much change from the time the primary archesporial cell is differentiated until about the time of pollination. About this time the nucellus begins to increase in size by the development of perisperm, and the diamond-shaped border of the cup increases in height around the developing fruit, until at maturity the fruit projects about one third of its length (FIG. 17). Sometimes the margin of the cup extends out practically as far as the outer end of the ripe fruit. The borders of these cups constitute ridges between the flowers, and the tops of these ridges and also the peduncle of the spike are rather thickly beset with simple, sharp-pointed hairs (FIG. 18). Each of these hairs consists of four to eight cells, including the basal cell, arranged uniserially, and measures from .15 mm. to .3 mm. in length. Among these hairs on the rachis and on the peduncle of the spike, and also on the carpels and bracts, there are glandular trichomes each consisting of three cells—a basal cell belonging to the epidermis, a short stalk-cell, and an enlarged terminal cell which usually has the shape of a much-flattened oblate spheroid, or door-knob (FIG. 18). As Haberlandt (26, pp. 444–455) suggests, these trichomes probably serve for the excretion of water (as hydathodes), or at least for the absorption of water. According to Solereder (69), hydathodes of this kind occur not only in *Peperomia*, but also in the related genera *Saururus* and *Piper*.

Large oil-cells are present in the rachis, bracts, and carpels. Starch grains are abundant in the rachis and bracts.

The anthers, as in all other species of *Peperomia*, are bilocular. The masses of archesporium in the stamen, when fully differentiated, show about twenty-five cells in cross-section. The tapetum, which is organized very early, consists of a single layer of cells. This layer entirely lines the pollen sac, and thus completely surrounds the male sporogenous tissue. At first it is rather thin, but the cells increase in size until they are quite large, reaching their greatest relative size about the time of the formation of the tetrads of microspores (FIG. 19). The walls of the pollen sacs are three cells thick—the epidermis, the endothecium, and a more or less complete and very thin layer inside the endothecium. This is exclusive of the tapetum. The microspores are formed by the time the primary archesporial cell in the nucellus of the same flower has cut off the parietal cell. The walls of the microspores immediately become somewhat thickened. The microspores, which are uninucleate at first, become binucleate before the nucleus of the embryo sac mother-cell of the same flower divides. The walls of the pollen grains increase in thickness, and become roughened on the outside. Their nuclei do not divide further before germination. The mature microspore is therefore binucleate, and no cross-wall is formed between the nuclei. The tapetum and the thin layer of cells just inside the endothecium have practically disappeared by the time the microspores have become binucleate and the endothecium has become fully developed. The pollen is shed sometime after the embryo sac of the same flower becomes eight-nucleate and before it becomes sixteen-nucleate. This is later than it occurs in *P. pellucida* (Johnson, 30). Very few pollen-tubes were seen, and none of those seen were in good condition. The details of the germination of the pollen were not made out.

The embryo sac and seed develop in a manner closely similar to that described by Campbell (6 and 7) and by Johnson (30) for *P. pellucida*. The primary archesporial cell is single and subepidermal (FIG. 1). It divides to form a tapetal cell, and the definitive archesporial cell,* or the embryo sac mother-cell, as it has sometimes been called (FIG. 2). At the time of this division of the primary archesporial cell, the integument has grown about half-way up to the apex of the nucellus. The tapetal cell by repeated division gives rise to a cap of parietal cells. This cap of tapetum becomes two or three cells thick before the nucleus of the embryo sac mother-cell divides, and three cell-layers in thickness is about the limit of its development (FIG. 3).

The reduction of chromosomes probably occurs in the first two divisions of the nucleus of the embryo sac mother-cell, as is indicated by the presence of synapsis before the first division (FIG. 5). In this respect the behavior is the same as that reported by Johnson for *P. hispidula*.

The nucleus of the embryo sac mother-cell divides into two (FIG. 6), and these two divide into four nuclei (FIGS. 7, 8), which usually at least are arranged tetrahedrally—that is, the four nuclei occupy the four corners of an imaginary tetrahedron (FIG. 7). The central part of the embryo sac, from this stage onward, is occupied by a large vacuole. As was shown by Brown (4) in *P. Sintenisii* and in *P. arifolia*, and by Brown and Sharp (5) in *Epipactis*, the nuclei resulting from the first two divisions of the nucleus of the embryo sac mother-cell are frequently separated by more or less complete rudimentary or evanescent walls (FIGS. 6, 8). It is possible that these rudimentary walls are always formed following the first two divisions of the nucleus of the embryo sac mother-cell, but that they are so evanescent that they are not often seen. No case was found in which the wall following the first division had persisted until the second division, and the walls following the second division, so far as observed, always disappeared before the third division in the embryo sac.

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* The definitive archesporial cell is to be distinguished from the primary archesporial cell which is the parent of the definitive archesporial cell plus the tapetal or parietal cell.

Each of the first four nuclei divides, thus giving rise to eight nuclei (FIG. 9), which are scattered in the peripheral layer of cytoplasm surrounding the large central vacuole. No signs of separating walls were seen at this stage.

Each of these eight nuclei divides, thus giving rise to sixteen free nuclei in the embryo sac, distributed in the same way as were the eight (FIG. 10). Soon after this stage is reached, a portion of the cytoplasm near the micropyle, together with a nucleus, is cut off by a wall from the rest of the sac, and becomes the oösphere or egg (FIGS. 13, 14). A smaller portion of the cytoplasm very near the egg, together with a nucleus, is cut off by a wall and becomes a synergid, the only one formed in the sac (FIG. 14). It is probable that the egg and synergid arise from sister nuclei, but no definite evidence of this was seen. Of the remaining nuclei, a number varying from six to eight in different embryo sacs is cut off singly from the rest of the embryo sac by saucer-shaped walls (FIG. 13). A small portion of cytoplasm is cut off with each of these nuclei. These peripheral nuclei, as they were called by Johnson (30), take no further part in development and finally degenerate, being crushed by the developing endosperm. The remaining nuclei, varying from six to eight in different embryo sacs, become grouped together, usually near the center of the embryo sac (FIG. 11), and fuse to form the endosperm nucleus (FIG. 12). The number of nuclei taking part in the formation of the endosperm nucleus, and consequently the number of peripheral nuclei left over, may vary to a greater extent than to the limits observed. The endosperm nucleus is formed in essentially the same manner as that of *P. pellucida* (Johnson, 30).

The embryo sac evidently enters upon a resting stage after four nuclei are formed and before these divide into eight. This is indicated by the fact that a much larger proportion of four-nucleate sacs were found in the preparations than of two-nucleate or eight-nucleate sacs. A number of slides, containing all stages from the definitive archesporial cell to the mature embryo sac, were carefully examined, and an accurate count made to determine this proportion, with the following result: *six* two-nucleate sacs, *thirty-five* four-nucleate sacs, and *seven* eight-nucleate sacs. The significance of this relation will be considered in the general discussion.

In nearly all the cases which were at a stage where this could be determined, it was observed that the endosperm nucleus divides before the male nucleus actually fuses with the nucleus of the egg (FIGS. 13, 14). In most instances, however, the male nucleus was present in the egg, where it usually remained for a considerable time before fusing with the egg nucleus. The presence of the male nucleus in the embryo sac may produce a stimulus which causes the endosperm nucleus to begin its development. This would seem to be in accord with Czapek's (15, p. 127) statement that the swelling of the ovary, in plants, after pollination, is caused by certain soluble substances (*hormones*) emanating from the pollen. The first division of the endosperm nucleus and all subsequent divisions of the resulting endosperm nuclei are mitotic, as is shown by the presence of typical spindles, etc. It is true that the equatorial plate is very broad in these spindles, a condition probably correlated with the presence of the large number of chromosomes contributed by the six or eight constituent nuclei fusing to form the endosperm nucleus, but this was not determined by counting.

Each division of the endosperm nucleus is followed by a cell-wall from the start, the first wall being parallel with the long axis of the fruit or nearly so (FIG. 13). The endosperm continues its development until, in the mature fruit, there is a mass showing about twenty-five cells in median longitudinal section (FIG. 16), and which is usually almost spherical in shape except for the depression in the micropylar side occupied by the undifferentiated embryo. The nucleus of each cell of the endosperm usually contains several nucleoli, the number observed varying from one to six.

After the male nucleus has fused with the nucleus of the egg, the development of the embryo begins. The fertilized egg divides to a two-celled embryo by a wall longitudinal to the nucellus (FIG. 15). The cells of the embryo continue to multiply until, in the apparently mature seed, there are about twenty cells in a median longitudinal section. The mature embryo shows no differentiation externally in any way except that it is somewhat flattened on the micropylar side. No suspensor is formed, and there is no indication of cotyledons or other organs (FIG. 16).

PEPEROMIA VERTICILLATA A. Dietr.

Peperomia verticillata A. Dietr., as used by C. de Candolle (9), is listed in the Index Kewensis as *P. pulchella* A. Dietr., while the name *P. verticillata* A. Dietr. is given as a synonym.

Part of the material for the study of this species was collected near Cinchona, Jamaica, where the plants grew on rocks and trees, at an elevation of 5,000 feet. But most of the material was collected in the greenhouse of The Johns Hopkins University from two plants which had been brought from Jamaica.

The flower-spikes of *P. verticillata* average fully three times as long as those of *P. reflexa*, with a range of two to nine centimeters in length. They are much less fleshy, and this condition, together with other characters of the plant, indicates that it is less strongly xerophytic in structure than the species first considered. The flowers, which are very similar to those of *P. reflexa*, are not nearly so closely crowded on the mature spike, but are loosely scattered along the axis. The bracts, trichomes, and oil-cells of the inflorescence axis resemble those of the former species. In this species the starch grains are strikingly abundant in the bracts.

The development of the stamen and pollen showed no essential difference from that of the former species, although the tapetal cells were larger and more conspicuous here (FIG. 19).

The development of the carpel and ovule, from the differentiation of the primary archesporial cell (FIG. 20) to the practically mature fruit, is essentially the same as in *P. reflexa*, except for some anomalous cases, which will be described later. The nucleus of the embryo sac mother-cell shows synapsis before it divides. Evanescent walls frequently more or less completely separate the nuclei in the two-nucleate and four-nucleate stages of the embryo sac. The mature embryo sac contains sixteen nuclei (FIG. 21). An egg and one synergid are cut off from the rest of the sac. Of the remaining fourteen nuclei, at least six are individually cut off as peripherals, and at least six others fuse together to form the endosperm nucleus. There can be very little doubt that the combined number of peripheral and endosperm nuclei is fourteen as it is in *P. reflexa*, and the number of each probably varies, as it does in that species.

As in *P. reflexa*, relatively many more four-nucleate embryo sacs were found than two-nucleate or eight-nucleate ones, thus indicating that there is a resting stage after the sac becomes four-nucleate.

The abnormal lobing of the ovules is the most interesting feature in the development of this species. A very large percentage of the ovules do not develop in the manner typical for this genus, but become more or less lobed (FIGS. 22–27). The carpel, which encloses an abnormal lobed ovule, seems altogether normal. The irregularity is confined to the nucellus and integument. Instead of the simple, ellipsoidal ovule, usual in *Peperomia*, we often have a two-lobed structure, one lobe developing an embryo sac and the other usually remaining sterile (FIGS. 23–27). The notch between the fertile and sterile lobes does not extend clear to the base of the ovule, but only about one half to three fourths of the distance (FIGS. 23, 27)—so that this lobing may be looked upon as a forking or branching of the ovule, somewhat similar to that reported by Hofmeister (29) in *Morus alba*.

The sterile lobe is generally larger than the fertile lobe, so that less than half of the tissue of the ovule takes part in the formation of the seed. The fertile lobe is the only part of the ovule which develops an integument (FIG. 25), and this integument may vary greatly. In normal, unlobed ovules the integument is two cells thick except at the apex where it is thicker around the micropyle.

In the abnormal, lobed ovules, it is frequently more than two cells thick, is usually irregular in shape, and is often more or less incomplete. The fertile lobe develops into a ripe seed, which is more or less deformed by the presence of the sterile lobe. The latter may cause a flattening of one side of the seed, or there may be a depression in one side of the seed due to its presence (FIG. 27). The sterile lobe is always more or less cut up into smaller lobes, and this subdivision is extremely irregular and often very complex. The sterile lobes often contain large oil-cells, which are regularly found in the carpels, bracts, and rachis, but are not present in the normal ovules, nor in the fertile lobes of these lobed ovules.

Frequently, in young ovules, one or more of these sterile lobes appear potentially able to form an embryo sac, as indicated by their shape, their affinity for certain stains, and sometimes by the presence of cells which appear to be sporogenous in character. In fact a few cases were found in which the two lobes of the ovule were fertile, each having an embryo sac and a separate integument. But no ovule was found in which more than one embryo had been initiated. In this respect, the phenomenon resembles the similar abnormality in *Morus alba* (Hofmeister, 29) in which, in all the investigated cases, the ovules aborted after the egg apparatus was formed.

The flower-spikes which showed this abnormality were all obtained from the two plants in the greenhouse at the Botanical Garden of The Johns Hopkins University. No such cases were found in the Jamaican material. It may be concluded that the greenhouse environment was responsible for the phenomenon, but this seems improbable when we take into consideration the fact that almost nothing of this kind was seen in the half dozen other greenhouse species which were studied in detail. On one plant of *P. verticillata*, which grew in the greenhouse, nearly one half of the ovules were of this lobed sort. In fact, in some spikes of this plant every ovule was lobed or branched. On the other plant, a very much smaller proportion of the ovules showed this abnormality.

Whether these abnormal structures have more than a teratological significance is difficult to determine. Their relative abundance may indicate that they have some phylogenetic suggestion. It may be an approach to a condition of more than one ovule in a carpel, and may be of atavistic significance.

More than one ovule in a carpel was the prevailing condition in the ancestors of the Piperaceae, if the theory of Lotsy (42, pp. 487–513) or of Hallier (27) be accepted, for both these authors believe that the Piperaceae have descended from the Magnoliaceae. Of this latter family of ten or eleven genera, all but one genus (*Illicium*) have more than one ovule in each carpel. And the same thing is true, if we accept the phylogenetic view embodied in the classification of the Engler-Gilg Syllabus (18, p. 157). The Saururaceae, which according to that grouping is the lowest family of the Piperales, has multiovulate carpels, and the carpels of certain of the Casuarinaceae, the family next below the Piperales, may sometimes contain two ovules.

Schwere (65), working on *Taraxacum*, found a case in which two embryo sacs developed in one nucellus, each giving rise to a normal embryo. Phylogenetically considered, he pointed out that we have here one megasporangium with two megaspores, and he considers it an atavistic appearance, an illustration of Hofmeister's ingenious and masterly work on the genetic relationship between Phanerogams and Cryptogams.

Hofmeister (29) considered the abnormal division of the nucellus in *Morus alba* as a monstrosity, although it was of frequent occurrence. The cases of *Morus* differ from those of *Peperomia* in that the two parts or lobes of the nucellus of the former are always both enclosed by the same inner integument, while in the latter the two parts or lobes of the nucellus are never enclosed by the same integument.

Braun (3) refers to these cases of *Morus* (Hofmeister, 29) as false polyembryony (*unächte Polyembryonie*), and they have been so classified by later authors (Ernst, 19; Coulter & Chamberlain, 14). The reason for this is not plain, for there is no statement in Hofmeister's brief description that any embryos were really initiated. Since no case was found in *P. verticillata*, in which more than one embryo was initiated in the ovule, it is inappropriate to consider this a case of polyembryony, or pseudopolyembryony, as it has been called.

In *Coffea arabica*, Hanausek (28) found actual polyembryony, as he called it, in which two to three embryos were formed in branches of the nucellus, one embryo developing in each branch. The abnormal branching of the nucellus in *Coffea* resembles that in *P. verticillata*, although the storage material in the former is endosperm, while in the latter it is chiefly perisperm.

This case of *Coffea*, that of *Taraxacum*, mentioned above, and other similar cases have been classed under pseudopolyembryony by later writers, but since they are cases of the occurrence of more than one embryo in a single seed, no good reason is apparent for calling the phenomenon *false* polyembryony. It is true that these cases, in which more than one embryo arises in one nucellus—each in a separate embryo sac—are quite different from the ordinary cases of polyembryony, but they do not differ from them in the essential character of polyembryony, that is, the initiation of more than one embryo in one ovule.

Two ovules, each surrounded by a separate inner integument, each containing an embryo sac, and both inside a common outer integument, were described and figured by Schacht (60, *pl. 3, f. 18*) in *Orchis Morio.* Braun (3) was of the opinion that these twin ovules, as he called them, arose by division of the nucellus, rather than by a growing together of two nucelli. He was led to this view by the appearance inside of the common outer integument of two entirely separate inner integuments.

In *Monotropa Hypopitys*, Schacht (60, p. 40) found a quite similar case, in which two embryo sacs filled with endosperm were surrounded by a single integument.

The case of *Orchis latifolia*, described and figured by Schleiden (62, p. 599, *pl. 6, f. 2*), is, as suggested by Strasburger (72), doubtless to be interpreted in the same way as Schacht's twin ovules in *Orchis Morio* (60).

Strasburger (72) described a case, similar to that found in *Orchis Morio*, in a closely related orchid, *Gymnadenia conopsea*, in which each of the two embryo sacs already contained an embryo.

Luerssen (43, p. 296) mentioned a similar case, which he found in *Iris sibirica.*

While the abnormally branched or lobed ovules in *Peperomia verticillata*, *Monotropa*, *Morus*, *Coffea*, *Iris*, *Gymnadenia*, and

Orchis resemble one another in the occurrence of two embryo sacs in one nucellus, there are, with respect to the integuments, at least four different classes: (1) That represented by *Peperomia* in which each fertile lobe of the nucellus has an independent single integument, (2) That represented by *Monotropa* in which both embryo sacs are surrounded by the same single integument, (3) That represented by *Morus*, the ovules of which have two integuments, in which both embryo sacs are within the same inner integument, (4) That represented by *Gymnadenia* and *Orchis* in which each lobe has a separate inner integument but both lobes are within a common outer integument. It seems that in cases like *Morus* and *Monotropa* we have two gametophytes developed within a single megasporangium, although divided or forked, for it is still all inside of the single integument, or inside the inner integument, if there be two. And it may be but a step from this to cases like *Peperomia* and *Orchis*, which, if they have more than teratological significance, probably either represent an approach to a condition of more than one ovule in a carpel, or they constitute atavistic appearances of a similar condition.

PEPEROMIA SCANDENS Ruiz & Pav.

The material for the study of *Peperomia scandens* Ruiz & Pav. was collected in the greenhouse of The Johns Hopkins University at Homewood, from a plant brought from Jamaica. In its native habitat, the plant commonly grows at low altitudes as an epiphyte upon the trunks of trees.

The flower-spikes of *P. scandens* are about the same length and about the same diameter as those of *P. reflexa*. The most obvious differences are that the mature fruits of the former are hardly at all sunk in the axis, while those of the latter are deeply sunk (FIGS. 4, 17, 32, 33), and that the fruits of the former have long, curved beaks, while those of the latter have only very short straight beaks. The carpel of *P. scandens* is sessile in the axil of a peltate bract, which closely resembles those of the two preceding species. Up to the sixteen-nucleate stage of the embryo sac, the carpel is sunk in the spike to such a depth that the stigma and beak of the carpel barely project outside the surface. At this stage, the stalk of the bract is entirely sunken in a separate cavity just below the one containing the carpel, only the shield-like top of the bract being outside. It is not until after the embryo sac is mature that the developing fruit is pushed out. The flowers and consequently the fruits are just about as much crowded in this species as they are in *P. reflexa*. There are no hairs on the rachis between the flowers as there are in *P. reflexa*, but there are a few on the peduncle of the spike. The absence of hairs on the rachis, together with the exserted fruits and thinner epidermis, indicates that this species is less xerophytic than *P. reflexa*. In all essential particulars the flowers and fruits of *P. scandens* closely resemble those of the two preceding species.

In the development of the stamen and pollen, this species very closely coincides with that of *P. verticillata*.

The development of the carpel and ovule, from the differentiation of the primary archesporial cell to the practically mature fruit, is essentially the same as in *P. reflexa*. The nucleus of the embryo sac mother-cell goes into synapsis before division. Evanescent cell-walls frequently appear between the nuclei following the first and second divisions in the embryo sac (FIGS. 28–31). The mature sac contains sixteen nuclei, of which one becomes the egg and one becomes the single synergid (FIG. 34). Of the remaining fourteen nuclei, a number varying from six to nine are cut off as peripherals, and there is little doubt that the endosperm nucleus is made up by the fusion of the remainder of the fourteen, although in many cases the number could not be positively determined.

The difficulty in determining the exact number of nuclei which fuse to make up the endosperm nucleus in any species of *Peperomia* studied by the writer, lies in the fact that usually, if not always, a part of the nucleoli fuse during the process of fusion of the nuclei. The nucleoli are excellent indicators of the number of component nuclei as long as they remain distinct. But it is comparatively rare that one finds in his preparations complete groups of fusing endosperm nuclei in which no nucleoli have yet fused. It is true that the lobes of the endosperm nucleus and the relative size of the nucleoli can frequently be relied upon to indicate to what extent fusion has proceeded, but not after the fusion is complete.

A resting stage evidently occurs in this species after the embryo sac has reached the four-nucleate stage, as shown by the relatively greater number of four-nucleate sacs than of two-nucleate or eight-nucleate ones. In forty-two ovules, taken at random, *ten* two-nucleate, *thirty* four-nucleate, and *twelve* eight-nucleate sacs were found.

PEPEROMIA METALLICA Lind. & Rod.

The material for the study of *Peperomia metallica* Lind. & Rod. was obtained from a plant growing in the greenhouse of The Johns Hopkins University at Homewood.

In the original description of this plant by Rodigas (58), there was no description of the flowers, and it seems that none has been published since.* In fact Linden and Rodigas were not absolutely sure that the plant was a *Peperomia*, although they named it and described it as such. The flowers, however, leave no doubt that the plant is a true *Peperomia*. They are borne on a spike, which varies from 3.5 cm. to 7.5 cm. in length, and which is rather slender, resembling that of *P. verticillata* in size, and the flowers are loosely scattered along the spike and are only slightly sunken in the axis. The rachis is smooth except for the presence of hydathodes very similar to those in the other species of *Peperomia*. The flower consists of two stamens and a single carpel, the latter being sessile in the axil of a peltate bract, which very closely resembles those of the other species of the same genus studied by the writer. The anthers are bilocular; the stigma is sessile and penicillate; and the carpel contains a single orthotropous ovule. In fact, the whole flower and all its parts closely resemble those found in other Peperomias.

The development of the carpel and ovule, from the differentiation of the primary archesporial cell up to the four-nucleate stage of the embryo sac, is essentially the same as that observed in *P. reflexa*. The nucleus of the definitive archesporial cell or embryo sac mother-cell shows synapsis before division.

A striking abnormality was observed in this species. The single plant, cultivated in the greenhouse of The Johns Hopkins University, when flowering in the autumn of 1912 bore only four or five spikes each of which was interrupted by a zone of small vegetative leaves, as shown in FIG. 35. Flowers are borne on the spike both above and below this zone of leaves, being more distant from each other just above the zone than they are below it. In other words, in the arrangement of the flowers, the part of the spike above the leaves as well as the part below the leaves resembles a whole normal spike of this species, that is, it is much as though there were one normal spike above another. In this respect these abnormal interrupted spikes remind one of the similar, though normal, phenomenon in *Callistemon*, the inflorescence axis of which continues to grow after flowering and produces a zone of vegetative leaves and later another zone of flowers, and so on. An approach to this condition is normally found in *Ananas sativa*, in which the inflorescence axis continues to grow and produces vegetative leaves above the fruits. This phenomenon has also been found as an abnormality in *Pinus* and *Larix*. But in neither of these cases, so far as known to the writer, is there a second zone of flowers formed, as there is in *Callistemon* and in *Peperomia metallica*.

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* Dr. Casimir de Candolle writes me that his unpublished manuscripts contain a diagnosis of this species including the flowers.

Dr. Casimir de Candolle writes me that these interrupted spikes are not present in his two herbarium specimens of *P. metallica*. And further, he thinks that the peculiar spikes constitute a teratological case, of which he has found striking examples in several species of *Piper*, and also in some Peperomias. In *P. Fraseri* C. DC. (*P. resedaeflora* Lind. & André), particularly, he has seen some spikes in which a few scattered bracts were replaced by small undeveloped vegetative leaves.

At a subsequent blooming of the plant in the greenhouse at Homewood, only six of the abnormal spikes appeared, while at least twice that number were normal. One of the abnormal ones showed the small vegetative leaves scattered considerably along the axis. A close examination of the interrupted zone shows that a few of the leaves have flowers in their axils.

The writer believes with De Candolle that these abnormal spikes have only teratological significance.

PEPEROMIA FRASERI var. RESEDIFLORA C. DC.

The flower-spikes of *Peperomia Fraseri* var. *resediflora* C. DC. (*P. resedaeflora* Lind. & André), which were used in this study, were collected by Professor D. S. Johnson in 1901 in the greenhouse of the "Pflanzenphysiologisches Institut" in Munich.

This species is peculiar for a *Peperomia*, in that it has compound flower-spikes. In the genus *Peperomia*, which comprises some four hundred species, nearly all have the flowers in simple spikes. But in this species the flowers are borne in conical panicles with a central axis and numerous lateral branches, the flowers being sessile in the axils of bracts and limited in their distribution to the branches of the inflorescence, except the apical portion of the central axis, as is usual in paniculate inflorescences.

The development of the carpel and ovule, from the definitive archesporial cell, or embryo sac mother-cell stage, up to the sixteen-nucleate embryo sac stage, coincides very closely with that of *P. reflexa*. In several cases rudimentary or evanescent walls were clearly visible in the two- and four-nucleate stages.

PEPEROMIA BLANDA HBK.

The material for the study of *P. blanda* HBK. was collected in the greenhouse of The Johns Hopkins University at Homewood.

The development of the embryo sac, from the embryo sac mother-cell stage to the 16-nucleate stage, closely resembles that of *P. reflexa*. Evanescent walls were seen in the two- and four-nucleate stages (FIG. 36). The number of peripheral nuclei cut off in the mature sac is about eight and seems to vary above and below this number.

This species differs from the others examined in this study, in that the stigma is both above and below the external opening of the stylar canal and is not limited to the anterior or lower part of the carpel.

Two cases were found in which the ovule was lobed in a manner similar to those of *P. verticillata*. And three cases were observed in which there were two ovules in one carpel. These lobed ovules and twin ovules doubtless have the same significance as the lobed ovules of *P. verticillata*.

Baillon (2, p. 140) calls attention to an approach to the anatropous condition in the ovules of this species and states that the ovule is inclined toward the anterior side of the ovary. An examination of a number of ovules, however, shows that this feature is not constant. In fact, the ovules are usually inclined toward the axis of the inflorescence, that is, toward the *posterior* side of the ovary, but the micropyle may be either anterior or posterior to the apex of the ovule.

PEPEROMIA GALIOIDES HBK.

The flower-spikes for the study of *P. galioides* HBK. were collected in the greenhouse of The Johns Hopkins University at Homewood. The plant from which they were obtained was collected near Cinchona, in the Blue Mountains of Jamaica, where it grew on the crags on the flank of John Crow Peak.

The development of the embryo sac, from the stage of the definitive archesporial cell, or embryo sac mother-cell, to the sixteen-nucleate embryo sac, is essentially the same as that of *P. reflexa.* Evanescent walls were seen in the four-nucleate stage.

PEPEROMIA LANGSDORFFII Miq. (?)

The material used in the study of *P. Langsdorffii* Miq. (?) was collected in the greenhouse of The Johns Hopkins University at Homewood. According to the Berlin Botanical Garden, the plant is a native of the West Indies and the northern part of South America.

The development of the embryo sac, from the embryo sac mother-cell stage to the two-nucleate embryo sac, is essentially the same as that of *P. reflexa.* Evanescent walls were observed in the two-nucleate embryo sac.

PIPER TUBERCULATUM Jacq.

The only species of the genus *Piper* examined in this study was the arborescent species *P. tuberculatum* Jacq. The flower-spikes were collected from a tree twenty feet in height, which was growing in the forest on the flanks of John Crow Peak at about 5,300 feet altitude, near Cinchona, in the Blue Mountains of Jamaica. Part of the material was collected and fixed in June, 1906, by Professor D. S. Johnson. The remainder was collected from the same tree by Mr. Jonas Walker, caretaker of the Cinchona Gardens, at intervals from July 8 to October 30, 1912, and as collected it was immediately put into a solution consisting of four per cent. formalin in seventy per cent. alcohol,* in which it remained for several weeks, after which time it was run up through the alcohols as though it had been fixed.

In this species the flower consists of four stamens and a single pistil, which is sessile in the axil of a short, club-shaped, hairy bract. At the apex of the ovary there are three short spreading stigmas, and this indicates that the pistil is compound, consisting in its morphological origin of three carpels. In each ovary there is borne a single, orthotropous ovule with two integuments (FIG. 41). The anthers are four-locular. There is no evidence—not even rudiments—of calyx or corolla. The flowers are borne on long slender spikes, which bear a close resemblance to those of many Peperomias.

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* The formula for this solution was kindly furnished to me by Dr. Charles J. Chamberlain.

The flowers are closely crowded on the spike. While it is true that they are initiated acropetally, they do not reach maturity in this succession, but all mature at practically the same time. In this latter particular they differ from those of the genus *Peperomia.*

The development of the embryo sac in *Piper tuberculatum* is closely similar to that described by Johnson (32 and 35) for *Piper medium*, *Piper umbellata*, and *Piper Betle* var. *monoicum.*

The primary archesporial cell is single and it is subepidermal (FIG. 37). This cell divides transversely, the upper cell being a parietal or tapetal cell, and the lower cell being the definitive archesporial cell (FIG. 38). The parietal or tapetal cell divides to form a layer four or five cells thick in the mature nucellus. The definitive archesporial cell develops directly into the embryo sac, without cutting off any megaspores.

The nucleus of the definitive archesporial cell, or embryo sac mother-cell (FIG. 39), divides to two (FIGS. 40, 41), and these two divide to four nuclei (FIG. 42). These divisions are not followed by walls, even evanescent ones. The nuclei of the embryo sac at the four-nucleate stage always have the linear arrangement or a close approach to it (FIG. 42). Not a single case of tetrahedral arrangement, as is found in *Peperomia*, was observed. Each of the four nuclei divides once more, giving rise to an eight-nucleate embryo sac, which contains an egg, two synergids, two polar nuclei, and three antipodals (FIG. 43). Thus it very closely resembles those found in other species of *Piper* and is typical of those found in the vast majority of angiosperms which have been investigated. There is some evidence that one of the male nuclei takes part in the formation of the endosperm nucleus.

[*To be concluded*]